Postembryonic Eye Growth in the Seashore Isopod *Ligia exotica* (Crustacea, Isopoda)

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Abstract. The eye of *Ligia exotica* is of the apposition type and has open rhabdoms. The facets are hexagonal, and the dioptric apparatus consists of a flat cornea and a spherical crystalline cone placed in the center of two large cone cells. Each ommatidium has seven regular retinula cells and one eccentric cell; a basement membrane forms the proximal boundary of the retina. With increases in body size from 0.6 to almost 4.0 cm, facet numbers and ommatidial diameters increased from 800 to 1500 and 35 μm to 100 μm, respectively; eye length and width grew from 1.2 to 3.2 and 0.9 to 2.5 mm, respectively; and length of dioptric apparatus and width of retinal layer changed from 70 μm to 180 μm and about 70 μm to 120 μm. Visual angles and interommatidial angles of centrally located ommatidia remained constant at about 30 and 6.9 degrees, respectively. An almost perfect linear relationship was found when eye length was plotted against the product between the square root of the total number of ommatidia and the ommatidial diameter. No difference between males and females was observed in any of the relationships, but the results suggest that, compared with smaller specimens, larger ones possess increased absolute sensitivity in single ommatidia, increased sensitivity to point sources, and overall larger angular visual fields for the eye in its totality. This means that larger individuals of *L. exotica* (which are also faster) have an advantage over smaller individuals at night, but that smaller individuals may cope better with bright lights. Vision in *L. exotica* seems useful not only in detecting poten-tial danger, but also in locating and approaching cliffs from a distance of 2–4 m when swimming in seawater.

Introduction

The eyes of the semiterrestrial isopod *Ligia exotica* have previously been the subjects of investigations into circadian changes (Hariyama *et al.*, 1986), ultraviolet responses (Hariyama *et al.*, 1993), and acceptance angles (Hariyama *et al.*, 2001). Because *L. exotica*, like most crustaceans, has inde-terminate growth, changes in eye size (possibly shape as well), facet numbers, and ommatidial dimensions must oc-cur as individuals undergo successive molting. The exis-tence of such growth-related changes in eye morphology suggests that at least some aspects of the way individuals of *L. exotica* see the world around them could depend on body size, age and, if males and females were of different size, even sex. Thus, one goal of this study was to examine the morphology of the eyes of a wide range of differently sized male and female *L. exotica*.

A second goal of this study was to examine postembry-onic changes (and their functional consequences) in the eyes of crustaceans in general and isopods in particular. Only one paper known to us lists ommatidial numbers in relation to an approximately 10-fold increase in body size in an isopod (Meyer-Rochow, 1982). Although Barlow (1952) provided details on the influence of the dimensions in apposition compound eyes on acuity and resolution and Horridge (1978) later added to these observations, few researchers of crustacean compound eyes, as documented by Meyer-Rochow and Reid (1996), ever mentioned the size or age of their experimental animals.

Investigations of postembryonic eye growth in crustaceans (*e.g.*, *Gammarus chevreuxi:* Bélehrádek and Huxley, 1930; *Panulirus longipes:* Meyer-Rochow, 1975; *Homarus gammarus:* Shelton *et al.*, 1981; *Procambarus clarkii:* Tokarski and Hafner, 1984; *Neomysis integer* and *Thysanoessa raschii:* Nilsson *et al.*, 1986; *Hemigrapsus sanguineus:* Eguchi *et al.*, 1989; Anomura: Fincham, 1988; *Petrolisthes elongatus:* Meyer-Rochow *et al.*, 1990, *Carcinus maenas* and *Hyas araneus:* Harzsch and Dawirs, 1996) show that crustacean compound eyes grow neither isometrically nor allometrically, but that certain eye components may follow their own separate growth patterns. In some cases, this leads to a change from one functional eye type to another, for instance, from the apposition to the superposition system in the rock lobster *Panulirus longipes* (Meyer-Rochow, 1975), the mysid *Neomysis integer*, and the euphausiid *Thysanoessa raschii* (Nilsson *et al.*, 1986). By examining certain aspects of postembryonic eye growth in *L. exotica*, we aim to better understand the role of vision in this species and the patterns governing size and age-related phenomena of vision in crustaceans generally.

Materials and Methods

Animals

Numerous individuals of *Ligia exotica*, representing a wide range of sizes, were collected by hand along the seashore of Shiogama (Miyagi Prefecture, Japan) at low tide around noon. On the same day, the captured specimens were taken to the laboratory in plastic containers and transferred to spacious tanks ($100 \times 40 \times 40$ cm). In the laboratory, the animals were maintained at a constant temperature of 24 °C under regular, cyclic light/dark conditions (L/D = 12/12 h) for about one week. During that time, they were fed commercially available dry pellets of insect food.

Measurements

The total number of ommatidia was determined from light micrographs and scanning electron micrographs of 24 eyes of differently sized animals (13 males and 11 females). Care was taken that only animals with seven pairs of legs were used in this investigation, since larvae of this species (usually reared under a female's abdomen in the marsupium, but occasionally dropping out or escaping from it) have only six pairs of legs. To count all the ommatidia of the curved and asymmetrically shaped eyes, each specimen was photographed from at least four angles. Debris particles on the eye's surface (Fig. 1C, white arrows) enabled us to identify individual ommatidia and thus allowed us to recognize the borders between adjacent micrographs. Ommatidia were counted from either the left or the right eye and in one case from both eyes.

Lengths and widths along the two principal axes of the compound eyes were determined from light micrographs of 13 male and 9 female specimens; the diameters of individual ommatidia from the dorsal non-rim area of the eyes were also measured. Eyes of 26 males and 13 females, frozen through rapid immersion in liquid nitrogen and then split with a razor blade, served as material for scanning electron microscopy (SEM). From the micrographs, facet diameters, lengths of dioptric structures, retinal widths, and interommatidial angles were measured. For each of these four features, depending on the condition of the specimen and the quality of the photographs, three to seven measurements per individual were taken. SAS statistical and graph software (SAS Institute Inc., Cary, NC) was used in curve constructions, calculations, and statistical analyses.

Specimen preparation

Out of several hundred individuals collected, 111 were randomly chosen (56 males and 55 females of various sizes) for this part of the study. Following confirmation of the sex through external inspection, each animal was weighed on an electric balance. To determine an animal's size (Fig. 1), four measurements were taken with a pair of dividers and a ruler calibrated to 1 mm: antennal length, uropod length, body length (excluding antennae and uropods), and total specimen length (including antennae and uropods). Any further observations, principally involving the eyes (see below), were carried out on material from these measured individuals.

For light microscopy, specimens were decapitated in the prefixative solution (2% paraformaldehyde and 2% glutaraldehyde in 0.1 M sodium cacodylate at pH 7.4) with a sharp razor blade. The surface of the compound eye was observed immediately thereafter under a light microscope (Nikon FX) by epi (= orthodromic) illumination. The light microscope (Zeiss Axiovar 100) was also used to pre-examine samples prepared for scanning electron microscopy and thick sections made with a cryostat. Semithin sections were stained in an aqueous solution of 1% toluidine blue.

For SEM, the eyes were surgically removed from the head while the latter was immersed in 0.1 M phosphate buffer (pH 7.2). The severed eyes were then fixed for 2 h in 2.5% glutaraldehyde in 0.1 M sodium cacodylate (pH 7.2). After the preparations were rinsed three times for 10 min in 0.1 M phosphate buffer, they were dehydrated in a graded series of ethanol and transferred into isoamyl acetate. The preparations were then dried with a critical point drying apparatus, attached to a metal plate, and ion-coated. To observe aspects of the longitudinal organization of the retina, some of the samples, after fixation, were frozen with liquid nitrogen, split longitudinally with a razor blade to expose the cleaved tissue layers, and dried and ion-coated with white-gold vapor (Eico ion coater IB-3) like the rest of the SEM samples. Observations were carried out under a Hitachi S-430 scanning electron microscope, operated at an accelerating voltage of 20 kV.
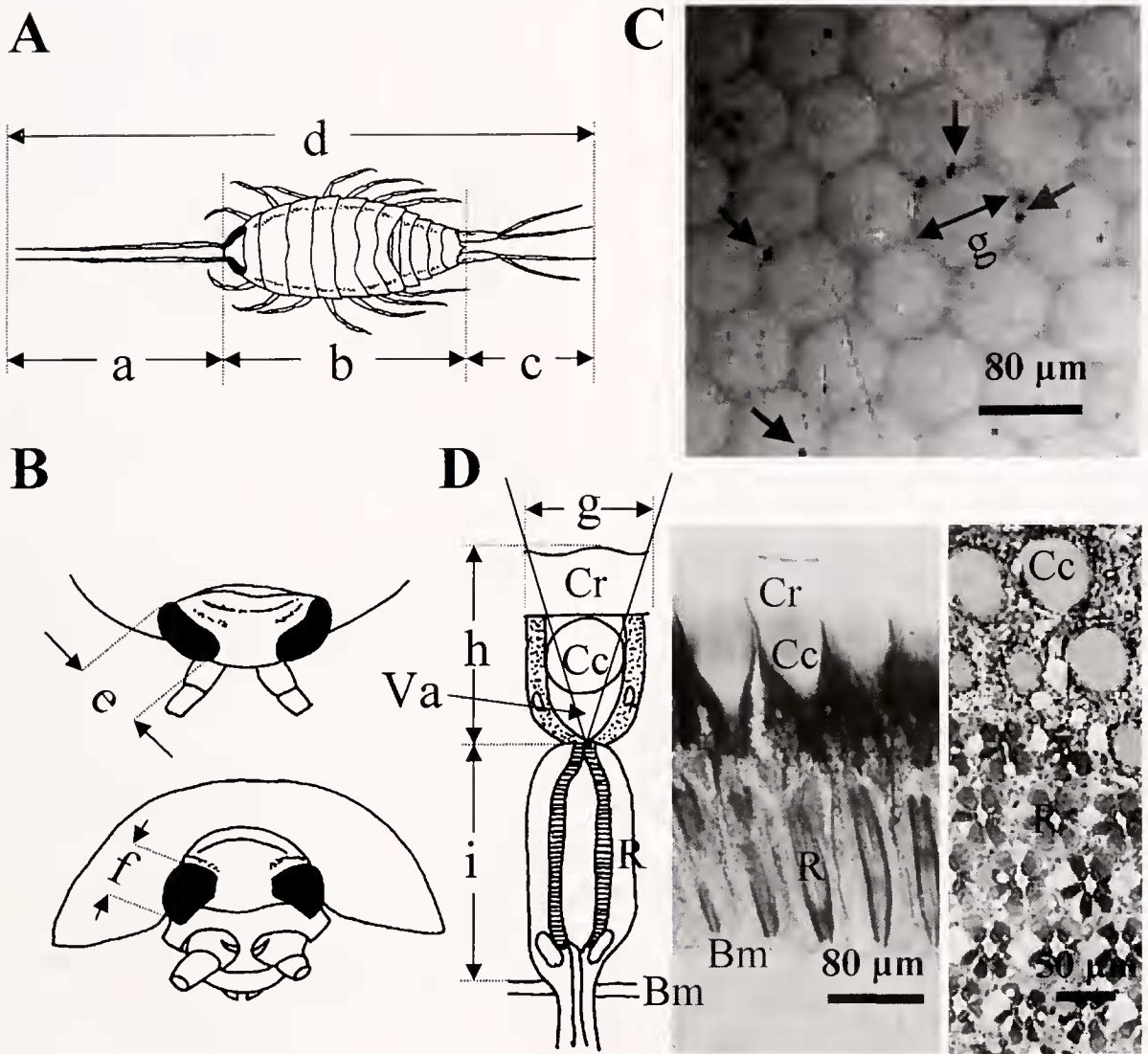
Figure 1. (A) Schematic drawing of *Ligia exotica* with the four lengths monitored indicated by small letters: (a) length of antennae, (b) length of body excluding antennae and uropods, (c) length of uropods alone, and (d) total body length. (B) Head region with eyes in black, viewed from above and showing horizontal (= anteroposterior) extent of eye measurable as e, and head region seen from the front with dorsoventral extent of the eye measurable as f. (C) Scanning electron micrograph of the outer surface of the compound eye of *L. exotica*, showing facets with hexagonal outlines. Ommatidial diameter was defined as the corner-to-corner distance (g), while debris on the cornea (white arrows) served as landmarks, assisting in identifying specific places on the eye. (D) Schematic drawing (left) and photomicrograph (right) of longitudinally sectioned ommatidia. Diameter of a facet was measured as g at the cornea (Cr), length of the dioptric apparatus, h, with the spherical crystalline cone (Cc) at its center, was defined as the distance from the corneal surface to the distal tip of the rhabdom, and the length of the retina, i, covered the distance between distal tip of the rhabdom (R) and basement (Bm). The angle Va defined the visual angle of an ommatidium.

Results

All individuals of *Ligia exotica* examined, irrespective of size, possessed apposition-type compound eyes with a hexagonal ommatidial lattice. The eyes were always sessile and occupied almost the entire lateral region of the head (Fig. 1A, B). The eyes were uniformly black; the ommatidial arrangement showed no obvious morphological differences, except for the marginal row of ommatidia all around the edge of the eye, in which smaller and seemingly immature ommatidia prevailed.
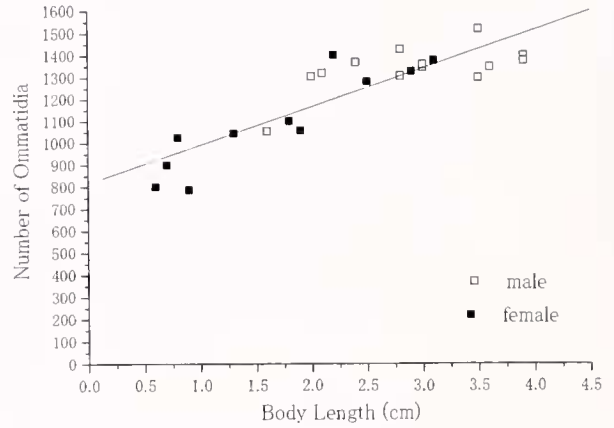
First we determined the relationship between individual weights and sizes. Size was used in preference to age, since (a) food quality and quantity as well as other environmental factors can affect the speed of growth in crustaceans, and (b)
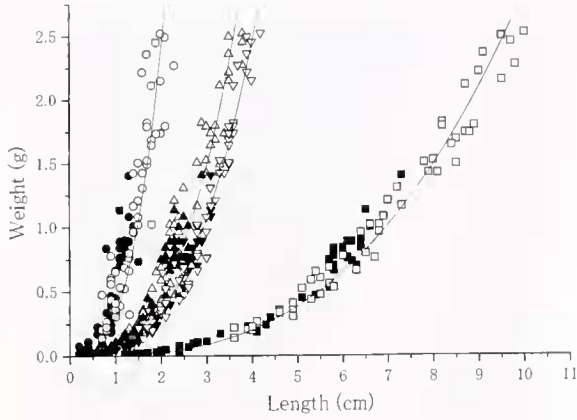
Figure 2. Relationship, obeying the function $y = kX^3$, between body weight (ordinate) and length of uropods (circles), antennae (triangles pointing upward), total body length (squares), and body length excluding antennae and uropods (triangles pointing downward) in male and female individuals of *Ligia exotica* (open and filled symbols, respectively). The values for k in the four relationships were calculated as 0.321, 0.062, 0.0038, and 0.045; the respective chi-square (χ^2) values were 0.104, 0.039, 0.016, and 0.011.


Figure 3. Relationship between number of ommatidia per single eye and body length in male and female *Ligia exotica*, obeying the formula $y = 174.3X + 816.4$ (SD = 104; $R = 0.87$).

we have no way of telling how old an individual really is and how many times it may have molted prior to capture. Lengths of the antennae, uropods, and bodies (with and without antennae and uropods) all increased with body weight (Fig. 2) and fitted the equation $y = kX^3$ (where y = weight, k = constant, and X = length). The largest individuals encountered were males of about 2.75 g in weight and about 11 cm in total body length (*i.e.*, measured with antennae and uropods). Females, being somewhat shorter and reaching a maximum total length of 7.5 cm and a weight of about 1.5 g (Fig. 2), appear to form a subpopulation of smaller individuals within the greater population of *L. exotica*. However, the shape and slope of the graph of the females' weight/size relationship were comparable to those of the males, provided we disregarded the upper (only males) and lower (only females) reaches. The smallest males weighed 0.14 g and measured 4.6 cm in total body length. Since the best correlation (*i.e.*, smallest variation) existed between weight and body length (defined as the length of an animal *excluding* antennae and uropods), we used body length alone (and not *total* body length) in all relationships regarding eye measurements and specimens of different sizes (see below).

The total number of ommatidia increased with an individual's increasing body length (Fig. 3). The smallest individuals (body lengths of *ca.* 0.75 cm) had about 800 ommatidia, whereas the largest specimens (body lengths *ca.* 4 cm) had about 1500. The increase in facet number between smallest and largest individuals was thus nearly two-fold, while body length increased at least five-fold. No statistical difference was detected between the curves of males and

females; both had a correlation coefficient for the least-squares fit of the data points of $R = 0.87$.

The extent of the horizontal and vertical spread of the eye was measured along the eye's two principal axes (Fig. 1B). The length of the eye along its horizontal (anteroposterior) extent and across its vertical (dorsoventral) range increased linearly with body size (Fig. 4). No obvious differences between the growth curves of male and female eyes were noticed, but eye growth in the anteroposterior direction slightly outpaced that of the dorsoventral direction. Thus, the general shape of the eye (but not its overall size) changed rather little throughout the animal's life.

The diameter of an individual ommatidium, measured either from the surface of the eye as facet diameter or from cross sections of the eye at corneal levels, increased nearly linearly with eye size and, when plotted against the body
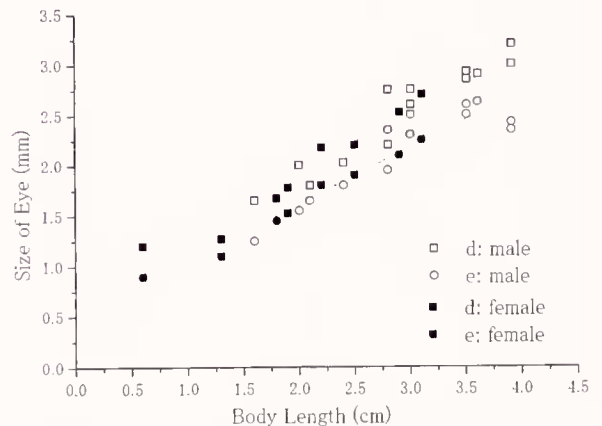
Figure 4. Length (anteroposterior: d) and width (dorsoventral: e) increases of the eye of *Ligia exotica* males and females in relation to body size. The equation $y = 0.65X + 0.62$ (SD = 0.144) describes the length relationship, while $y = 0.56X + 0.5$ (SD = 0.16; $R = 0.95$) describes the width relationship.
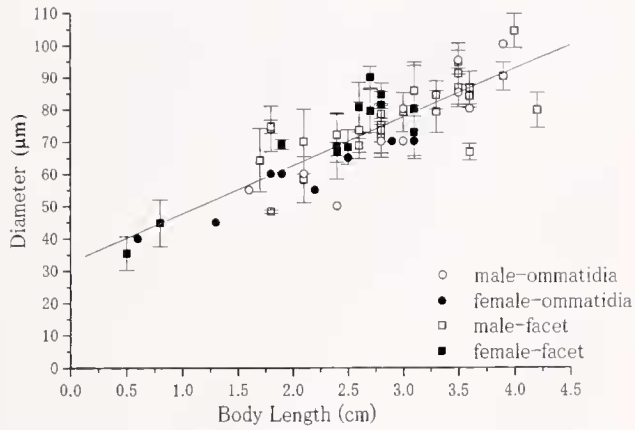
Figure 5. Relationship, obeying $y = 15X + 32.7$ (SD = 7.7; $R = 0.85$) between body length and ommatidial diameters, the latter either determined directly from scanning electron micrographs (single values) or as the average of 3–7 measurements taken from each longitidinally sectioned eye (values with standard deviation bars) of male and female specimens.
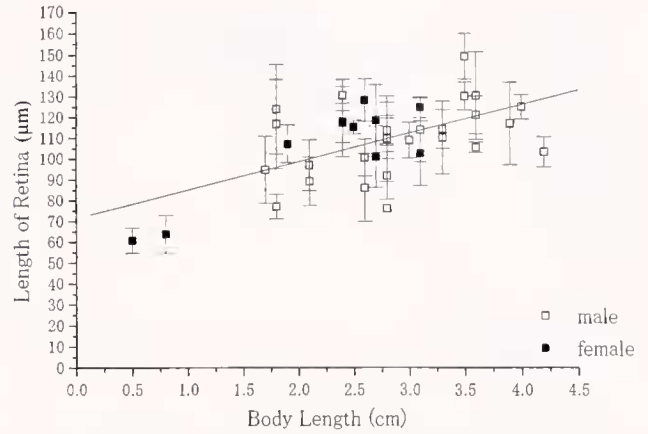
Figure 7. Relationship, obeying $y = 13.5X + 71.5$ (SD = 15.3), between body length and ommatidial length of retina, determined as the average of 3–7 measurements taken from each longitudinally sectioned eye of male and female specimens.

length of an animal, with growth of the whole animal as well (Fig. 5). The smallest and the largest specimens examined exhibited facet diameters of 35 μm and 105 μm, respectively. Once again, there were no differences between male and female individuals. The length of the dioptric structures (h in Fig. 1D) for both male and female individuals increased linearly in relation to body length of an animal (Fig. 6). The width of the retinal layer, measured as retina length per ommatidium in the eye of both males and females, also increased in relation to greater individual body size (Fig. 7), but with more variability ($R = 0.586$) than some other structures of the eye, for example, the layer of the dioptric elements mentioned earlier (see above).

True interommatidial angles cannot be obtained in *L. exotica*, because rhabdomeres are frequently skewed and the
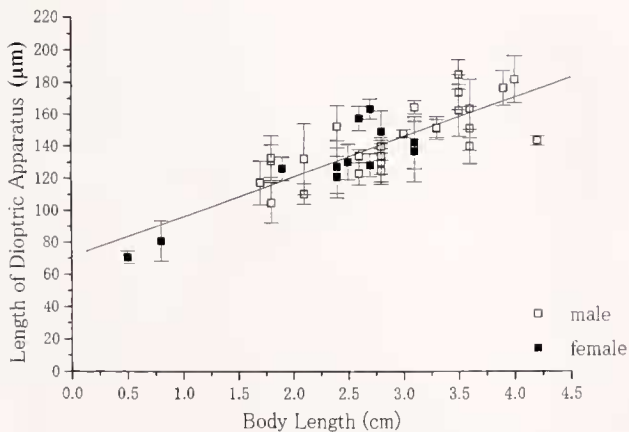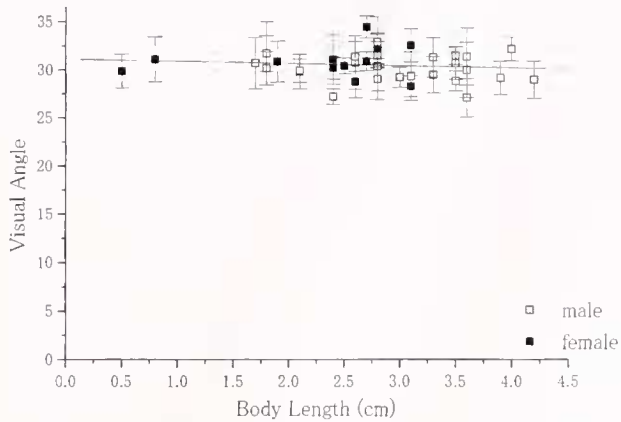

Figure 6. Relationship, obeying $y = 24.8X + 71$ (SD = 13.55; $R = 0.831$) between body length and length of dioptric apparatus, determined as the average of 3–7 measurements taken from each longitudinally sectioned eye of male and female specimens.

axes of ommatidial groups of retinula cells are not always parallel to the axes of the dioptric structures. Since the spacing of the facets is an important parameter in vision, two alternative angles, which are probably independent from each other, were measured. Dioptric systems of neighboring ommatidia, involving only cornea and cone cells, were usually straight. It was thus possible to measure the inclination of the axes through the dioptric structures of neighbouring ommatidia in 11 females and 16 males, ranging from 1 to 6 cm in body length. The interommatidial angle obtained in this way was 6.91° ± 0.95 and showed no appreciable difference across the size range of animals or between male and female. The second approach we used to examine interfacetal constancy involved what we termed *the visual angle*. This angle is *not* identical to the interommatidial angle, but it provides an estimate of the optical "catchment" of each dioptric apparatus on purely geometric grounds. It was measured on longitudinal sections as the figure formed by the two lines leading from the outer edges of the cornea to a common point at the proximal end of the crystalline cone (*cf.* Fig. 1D). Corneal surfaces and crystalline cone cells were arranged at right angles to each other, and facet diameters in both males and females increased in relation to body size. The dioptric elements in the ommatidia, however, also increased in size and became thicker and longer. Since the ratio between diameter and length remained more or less constant as *L. exotica* grew, the visual angles, representing optical catchment per ommatidium, also remained basically the same (*i.e.,* 30°) for different body lengths (Fig. 8).

Discussion

In contrast to the embryological morphogenesis of the crustacean compound eye (Fincham, 1984, 1988; Hafner

Figure 8. Relationship, obeying $y = -0.25X + 31.1$ (SD $= 1.53$) between body length and visual angle, determined as the average of 3–7 measurements taken from each micrograph of longitudinally sectioned eye of male and female specimens.

and Tokarski, 1998), postembryonic eye differentiation presents a far less uniform picture. The variety of patterns seen in different crustaceans reflects the wide range of tasks a compound eye has to carry out. Cases are known in which larvae possess eyes, but adults are eyeless and have lost their photoreceptors (*e.g.*, *Troglocaris anophthalmus:* Christian Juberthie, CNRS, Laboratoire souterrain, pers. comm., and Juberthie-Jupeau, 1972; *Alvinocaris markensis:* Chamberlain, 2000); or in which juvenile individuals feature apposition eyes, but adults have superposition eyes (*e.g.*, *Panulirus longipes:* Meyer-Rochow, 1975; mysids and euphausiids: Nilsson *et al.*, 1986); or in which the dioptric elements are lost and the retina changes from the imaging type to a nonimaging one (bresiliid shrimps: Gaten *et al.*, 1998). Obviously, such changes must have an effect on the more central components of the visual system; however, apart from a study of the optic ganglia of two brachyuran species by Harzsch and Dawirs (1996), no other detailed information on the events in the eyestalk ganglia during postembryonic compound eye maturation is available, and specifically for *L. exotica,* only a basic study of the optic neuropils (Sharma, 1982) has been published.

Not surprisingly, in view of the rather similar ecological requirements and behavior of the different size classes of *L. exotica,* postembryonic eye development in this species is less dramatic than that of the crustaceans mentioned in the preceding paragraph. The eye and most of its components grow isometrically, although the slopes of the growth curves for different structures, as our observations have shown, need not be identical. Through the addition of ommatidia following molts, interommatidial angles of the central region of the eye frequently decrease (*e.g.*, *Hemigrapsus sanguineus:* Eguchi *et al.*, 1989; *Carcinus maenas* and *Hyas araneus:* Harzsch and Dawirs, 1996), allowing the animal to develop greater resolving power in that part of the

eye. On the other hand, interommatidial angles can remain constant (*Petrolisthes elongatus:* Meyer-Rochow *et al.*, 1990) or may even increase with the addition of extra ommatidia (*Argulus foliaceus:* Madsen, 1964), depending on where in or around the eye the proliferation zone or zones exist. In *L. exotica,* ommatidia closest to the edge, all around the eye, displayed smaller and more irregular facet outlines than those of the central region. Ultrastructurally they also differed, but we have just begun to investigate whether a distinct proliferation zone is responsible for the recruitment of these marginal ommatidia and to what extent they can transform themselves into the more regular type. We noticed that the increase in ommatidia with age was neither strictly linear, as in the amphipod *Gammarus chevreuxi* (Bélehrádek and Huxley, 1930), nor exponential, as in *Petrolisthes elongatus:* Meyer-Rochow *et al.*, 1990). Because the number of the ommatidia in *L. exotica* appears to be correlated with the area of the compound eye (rather than simply with the size of the animal), we calculated the product of the square root of the total number of ommatidia and the average ommatidial diameter, plotting the values against the maximum length of the eye. The result is an almost perfect linear relationship (Fig. 9), suggesting that image quality (resolution) remains constant as the eye increases in size. When the growth relationship is expressed in this way, it becomes independent of an individual's age or molt status, which is an advantage because age and size in crustaceans cannot easily be connected (Shelton *et al.*, 1981).

L. exotica is an alert and agile species, and—as anyone who has tried to catch live specimens on a beach, whether during the day or under twilight conditions, would testify—it has keen eyesight. Electrophysiological recordings from adult animals, in air, confirm that acuity is impressive and that the acceptance angle of a single receptor cell is
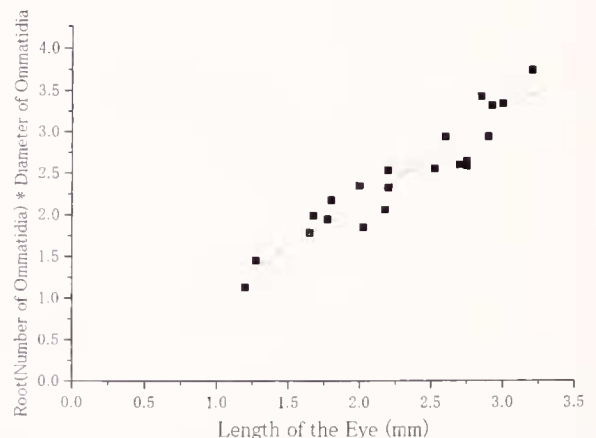
Figure 9. Plotting the product of the square root of total number of ommatidia and ommatidial diameter against eye length results in an almost perfect linear relationship, following the equation $y = 1.0X - 7.7$.

about 2°, even at night when sensitivity increases 10-fold (Hariyama *et al.*, 2001). Apparently, however, *L. exotica*, not only can see in air, but also can use vision underwater, for example, in attempts to reach coastal rocks or the shore from distances of 0.5–1.0 m (Taylor and Carefoot, 1990). Since this species undoubtedly had aquatic ancestors, and crustaceans are known to be able to use underwater visual landmarks (Cannicci *et al.*, 2000), we have to consider the possibility that some of the eye's functions as well as its structural characteristics (Richter, 1999) are rooted in *L. exotica's* behavior in the aquatic environment.

L. exotica can feed and survive submerged in seawater for at least 14 days, but small as well as large individuals immediately seek to reach the shore after being blown into the sea by a gust of wind or after accidentally jumping into the water as part of an escape maneuver (Taylor and Carefoot, 1990). At night, in total darkness, Taylor and Carefoot (1990) did not notice any swimming orientation that differed from randomness; most of the individuals tossed into the water sank to the bottom, where they would slowly crawl up the slope, presumably making use of leg proprioceptive inputs (Nalbach *et al.*, 1989). During the day, however, waterborne individuals tended to swim at the surface, and the chief factors influencing their directional surface-swims appeared to be "angle of sun and darkness of bottom or wall" (Taylor and Carefoot, 1990). Yet the same researchers pointed out that orientation to the sun "was of secondary importance" and that differentiation between lighter and darker features apparently provided the principal navigational cues.

In addition to spatial resolution and sensitivity, another important photoreceptor property that, according to Frank (1999), needs to be considered in "any comprehensive analysis of the visual system of organisms" is flicker fusion frequency (= temporal resolution). The latter is generally high in terrestrial and rapidly moving, daytime-active species and lower in aquatic organisms. Flicker fusion frequency (FFF) is not known in *L. exotica*, but Ruck and Jahn (1954) measured an average FFF of 120 in adults of the closely related *L. occidentalis*. Resembling that of the bumblebee eye (Meyer-Rochow, 1981), such a relatively high FFF value is not unusual for flying insects, but it is unusual for crustaceans (*cf.* Frank, 1999); it is probably related to the great speed with which all *Ligia* spp. scuttle around on the beach. Autrum (1950) showed that fast-moving arthropods require higher FFFs than slow-moving ones; and Srinivasan and Bernard (1975) showed that at angular velocities above a critical value, the temporal properties of an eye begin to determine spatial resolution to a greater extent than the optics of the eye do. Figures for running speeds of *L. exotica* individuals of different sizes are unavailable, but swimming speeds have been measured: animals 10–15 mm in body length are capable of velocities corresponding to about 3 body lengths/s, but individuals of 40–50 mm are faster and

cover 4–5 body lengths/s (Taylor and Carefoot, 1990). On that basis, we tentatively conclude that, unlike bigger specimens of *Ligia*, small ones do not need a high FFF value. We see confirmation for this notion in the ommatidial organization of the eye of the smaller specimens, which seemingly favors spatial resolution.

Since the shape of the eye in *L. exotica* stays roughly the same, density and contours of individual ommatidia are kept constant, and both interommatidial and visual angles persist unchanged throughout an individual's life; hence the resolving power of the eye should also remain rather stable, even if the FFF were to rise as the animal grows and becomes faster. With no significant change to the overall form of the compound eye in *Ligia*, we would expect the overall visual field of an eye to remain about the same throughout life. In small specimens, the visual fields of photoreceptor cells are, however, difficult to measure, and only recordings from larger individuals have been successful (Hariyama *et al.*, 2001). But because their facets are fewer as well as smaller, the eyes of younger specimens are likely to be less sensitive to point sources as well as extended sources of light (Land, 1981). Bigger specimens, with their more numerous facets and wider ommatidia, thus ought to have an advantage when it comes to exploiting dimmer environments. The ability to distinguish minor differences in contrast fits well with the observation by Taylor and Carefoot (1990) that bigger specimens of *L. exotica* will swim longer (25 s *versus* 16 s) and faster than smaller ones. Thus, larger *L. exotica* individuals can detect (and attain) a goal from a greater distance (as far as 3 m according to Taylor and Carefoot, 1990) than can smaller ones with less sensitive eyes.

The inability to see a rock or a cliff in the distance could actually be an advantage for a smaller individual because its swimming speed and endurance would be insufficient to allow it to reach such a far-off goal. A similar situation is seen in the intertidal halfcrab *Petrolisthes elongatus*, a species whose postembryonic eye-growth patterns resemble those in *L. exotica* (Meyer-Rochow *et al.*, 1990). When crabs of this species are robbed of their shelters, they immediately look for a new shelter. Larger individuals preferentially crawl towards boulders at greater distances, whereas smaller individuals seek out nearby ones, even if the sizes of the near and far boulders subtend the same degree of arc within the visual field of the crabs (Meyer-Rochow and Meha, 1994). Because the smaller crabs tire faster and are slower, an ability to visually perceive attractive boulders in the far distance (distance perception in the ant *Myrmecia nigriceps* was found to be 80 cm: Eriksson, 1985) would be wasted on them and, in fact, could leave them exposed to predators for dangerously long periods if they attempted to reach the distant target.

On the other hand, prolonged exposures to bright lights are generally much better tolerated by arthropods with smaller and strongly curved eyes (Kelber, 2000). Compared

with the larger eyes of fully grown individuals, the smaller eyes and narrower ommatidia in small *L. exotica* admit considerably less light to the photoreceptive membranes, thus reducing the risk of light-induced photoreceptor damage (Meyer-Rochow, 1994; Meyer-Rochow *et al.*, 2002). By requiring more (or brighter) light than large specimens to see, small individuals are predisposed to exploit the daytime hours. Although larger adults are also active during that part of the day, they are more cautious and more inclined to hide than the youngsters. At night the situation is reversed: the largest individuals with the most sensitive eyes are out and active, presumably relying on their improved vision to detect disturbances and the approach of danger even in semidarkness.

L. exotica is not the only peracarid crustacean that behaves in this way. The aquatic isopod *Idotea baltica* shows a growing preference with age for a dark background and night feeding (Merilaita and Jormalainen, 2000). Similarly, small juvenile shore talitrids are active under bright conditions but become increasingly dark-active as they age and grow (Rüppell, 1967). Even in the terrestrial isopod *Scyphax ornatus*, it is the adults that make lengthy foraging excursions at night (Quilter and Lewis, 1989). One might argue that it is not vision but humidity that governs activity periods and the place on the beach where shore crustaceans assemble. If, however, that were the case in *L. exotica* and the talitrids, cited above, smaller individuals—in greater danger of desiccation than larger ones—should come out predominantly at night, while bigger individuals should be more active during the day. Clearly, the need for moisture alone cannot explain the size-related exposure differences; a link with the anatomical organization of the eye and its functional limitations seems a considerably stronger explanation.

Acknowledgments

Literature Cited

Autrum, H. 1950. Die Belichtungspotentiale und das Sehen der Insekten (Untersuchungen an *Calliphora* und *Dixippus*). *Z. Vgl. Physiol.* 32: 176–227.

Barlow, H. B. 1952. Size of ommatidia in apposition eyes. *J. Exp. Biol.* 29: 667–674.

Bélehrádek, J., and J. S. Huxley. 1930. The rate of eye-growth and its variation in *Gammarus chevreuxi*. *J. Exp. Biol.* 7: 37–40.

Cannicci, S., C. Barelli, and M. Vannini. 2000. Homing in the swimming crab *Thalamita crenata*: a mechanism based on underwater landmark memory. *Anim. Behav.* 60: 203–210.

Chamberlain, S. C. 2000. Vision in hydrothermal vent shrimp. *Philos. Trans. R. Soc. Lond. B* 355: 1151–1154

Eguchi, E., K. Arikawa, S. Ishibashi, T. Suzuki, and V. B. Meyer-Rochow. 1989. Growth-related biometrical and biochemical studies of the compound eye of the crab *Hemigrapsus sanguineus*. *Zool. Sci.* 6: 241–250.

Eriksson, E. S. 1985. Attack behaviour and distance perception in the Australian bulldog ant *Myrmecia nigriceps*. *J. Exp. Biol.* 119: 115–131.

Fincham, A. A. 1984. Ontogeny and optics of the eyes of the common prawn *Palaemon serratus* (Pennant, 1777). *Zool. J. Linn. Soc.* 81: 89–113.

Fincham, A. A. 1988. Ontogeny of anomuran eyes. *Symp. Zool. Soc. Lond.* 59: 123–155.

Frank, T. M. 1999. Comparative study of temporal resolution in the visual systems of mesopelagic crustaceans. *Biol. Bull.* 196: 137–144.

Gaten, E., P. J. Herring, P. M. J. Shelton, and M. L. Johnson. 1998. Comparative morphology of the eyes of postlarval bresiliid shrimps from the region of hydrothermal vents. *Biol. Bull.* 194: 267–280.

Hafner, G. S., and T. R. Tokarski. 1998. Morphogenesis and pattern formation in the retina of the crayfish *Procambarus clarkii*. *Cell Tissue Res.* 293: 535–550.

Hariyama, T., V. B. Meyer-Rochow, and E. Eguchi. 1986. Diurnal changes in structure and function of the compound eye of *Ligia exotica* (Crustacea, Isopoda). *J. Exp. Biol.* 123: 1–26.

Hariyama, T., Y. Tsukahara, and V. B. Meyer-Rochow. 1993. Spectral responses, including a UV-sensitive cell type, in the eye of the isopod *Ligia exotica*. *Naturwissenschaften* 80: 233–235.

Hariyama, T., V. B. Meyer-Rochow, T. Kawauchi, Y. Takaku, and Y. Tsukahara. 2001. Diurnal changes in retinal cell sensitivities and receptive fields (two-dimensional angular sensitivity functions) in the apposition eyes of *Ligia exotica* (Crustacea, Isopoda). *J. Exp. Biol.* 204: 239–248.

Harzsch, S., and R. R. Dawirs. 1996. Maturation of the compound eyes and eyestalk ganglia during larval development of brachyuran crustaceans *Hyas araneus* L. (Decapoda, Majidae) and *Carcinus maenas* L. (Decapoda, Portunidae). *Zoology* 99: 189–204.

Horridge, G. A. 1978. The separation of visual axes in apposition compound eyes. *Philos. Trans. R. Soc. Lond. B* 285: 3–59.

Juberthie-Jupeau, L. 1972. L'alimentation des cinq premiers stades de *Troglocaris anophthalmus*— donnés biologiques et histologiques. *Ann. Speleol.* 27: 221–227.

Kelber, A. 2000. Eyes up. *New Sci.* 166: 93.

Land, M. F. 1981. Optics and vision in invertebrates. Pp. 471–492 in *Vision in Invertebrates: Handbook of Sensory Physiology*, Vol. VII/6B, H. Autrum, ed. Springer, New York.

Madsen, N. 1964. The anatomy of *Argulus foliaceus* Linné. *Lunds Universitets Arsskrift N.F. Avd. II* 59: 1–32.

Merilaita, S., and V. Jormalainen. 2000. Different roles of feeding and protection in diel microhabitat choice of sexes in *Idotea baltica*. *Oecologia* 122: 445–451.

Meyer-Rochow, V. B. 1975. Larval and adult eye of the Western rock lobster *Panulirus longipes*. *Cell Tissue Res.* 162: 439–457.

Meyer-Rochow, V. B. 1981. Electrophysiology and histology of the eye of the bumblebee *Bombus hortorum* (L.) (Hymenoptera: Apidae). *J. R. Soc. N. Z.* 11: 123–153.

Meyer-Rochow, V. B. 1982. The divided eye of the isopod *Glyptonotus antarcticus*: effects of unilateral dark adaptation and temperature elevation. *Proc. R. Soc. Lond. B* 215: 433–450.

Meyer-Rochow, V. B. 1994. Light-induced damage to photoreceptors of spiny lobsters and other crustaceans. *Crustaceana* 67: 97–111.

Meyer-Rochow, V. B., and W. P. Meha. 1994. Tidal rhythm and the role of vision in shelter-seeking behavior of the half-crab *Petrolisthes elongatus* (Crustacea: Anomura: Porcellanidae). *J. R. Soc. N. Z.* 24: 423–427.

Meyer-Rochow, V. B., and W. A. Reid. 1996. Does age matter in studying the crustacean eye? *J. Comp. Physiol. B* 166: 319–324.

Meyer-Rochow, V. B., D. Towers, and I. Ziedins. 1990. Growth patterns in the eye of the halfcrab *Petrolisthes elongatus* Milne-Edwards. (Crustacea: Decapoda: Anomura). *Exp. Biol.* 48: 329–340.

Meyer-Rochow, V. B., T. Kashiwagi, and E. Eguchi. 2002. Selective photoreceptor damage in four species of insects induced by experimental exposures to UV-irradiation. *Micron* 33: 23–31.

Nalbach, H.-O., J. Zeil, and L. Forzin. 1989. Multisensory control of eye-stalk orientation in space: crabs from different habitats rely on different senses. *J. Comp. Physiol. A* **165:** 643–649.

Nilsson, D. E., E. Hallberg, and R. Elofsson. 1986. The ontogenetic development of refracting superposition eyes in crustaceans: transformation of optical design. *Tissue Cell* **18:** 509–519.

Quilter, C. G., and R. D. Lewis. 1989. Clock control of foraging in the isopod *Scyphax ornatus* Dana. *N. Z. J. Zool.* **16:** 373–382.

Richter, S. 1999. The structure of the ommatidia of the Malacostraca (Crustacea)—a phylogenetic approach. *Verh. Naturwiss. Ver. Hamburg NF* **38:** 161–204.

Ruck, P., and T. L. Jahn. 1954. Electrical studies on the compound eye of *Ligia occidentalis*. *J. Gen. Physiol.* **37:** 825–849.

Rüppell, G. 1967. Tagesrhythmische und langfristige Faunenverschiebungen im marinen Supralitoral. *Z. Morphol. Ökol. Tiere* **60:** 338–375.

Sharma, S. P. 1982. Microanatomical studies on the optic neuropiles of an isopod, *Ligia exotica* Roux (Crustacea). *Folia Morphol.* **30:** 70–75.

Shelton, P. M. J., R. G. J. Shelton, and P. R. Richards. 1981. Eye development in relation to moult stage in the European lobster *Homarus gammarus* (L.). *J. Cons. Int. Explor. Mer.* **39:** 239–243.

Srinivasan, M. V., and G. D. Bernard. 1975. The effect of motion on visual acuity of the compound eye: a theoretical analysis. *Vision. Res.* **15:** 515–525.

Taylor, B., and T. Carefoot. 1990. Underwater survival, orientation, and locomotory ability in the semiterrestrial Japanese "funamushi" *Ligia exotica* (Roux). Pp. 121–130 in *Third International Symposium on Biology of Terrestrial Isopods,* University of Poitiers Publ., Poitiers, France.

Tokarski, T. R., and G. S. Hafner. 1984. Regional morphological variations within the crayfish eye. *Cell Tissue Res.* **235:** 387–392.